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Post-fire juvenile period of plants in south-west Australia forests and implications for fire management

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Abstract

Regular prescribed burning to manage the accumulation of flammable live and dead vegetation (fuel) is a strategy for ameliorating wildfire impacts in fire-prone environments. The interval between prescribed fires needs to be sufficient to manage fuel accumulation but it should also be ecologically acceptable. Time to first flowering after fire (juvenile period) is a biological indicator that can be used to guide minimum intervals between fires to conserve plant diversity. A survey of 639 plant species in forests and associated ecosystems of south-west Western Australian revealed that 97% of understorey species reached flowering age within 3 years of fire and all species reached flowering age within 5 years of fire. Within species variation was evident, with plants at the drier end of their range taking longer to reach flowering age. Fire sensitive plants, being obligate seeder species with longer juvenile periods (> 3 years), mostly occurred in low rainfall zones so took longer to mature, or in habitats that were less prone to fire because they remained moist for a longer period or because surface fuels were inherently sparse and discontinuous. Due to uncertainty about the reproductive biology and seed bank dynamics of most of the flora, we recommend that the conservative minimum interval between fires that are lethal to fire sensitive plants is about twice the juvenile period of the slowest maturing species in the community. Occasional landscape fires at shorter intervals would be ecologically acceptable only if these fires were of a sufficiently low intensity as to not kill plants with long juvenile periods, or were patchy and did not burn the habitats in which they occur.

Keywords: fire, juvenile period, seeders, resprouters, prescribed burning

Introduction

Plant communities in the south-west forest region of Western Australia display a remarkable array of physical and biological traits that enable them to persist in a fire prone environment, and in some cases depend upon fire for structural and floristic diversity (*e.g.*, Gardner 1957, Christensen and Kimber 1975, Christensen and Abbott 1989 and Burrows and Wardell-Johnson 2003). Fire regime is the history of fire frequency, season and intensity (Gill 1981) with fire frequency affecting both the structure of the vegetation and its floristic composition (Muir 1987, Burrows and Wardell-Johnson 2003). Fire frequency also directly influences fire intensity because the quantity of live and dead vegetation, which becomes fuel for a bushfire, accumulates rapidly in the first 10 years after fire, after which the rate of fuel accumulation slows (Burrows 1994, McCaw *et al.* 1996).

Today, intense summer wildfires threaten human life, destroy property and damage forest values such as timber and amenity. Large, intense wildfires can also be environmentally damaging and present a threat to ecosystem processes and conservation values including old growth forests, communities and species sensitive to high fire intensities, and extant populations of rare flora and fauna (see Abbott and Burrows 2003). Fire intensity, or the rate of heat energy release, is a measure of the severity of the fire; its damage potential, suppression difficulty and killing power. Wildfires derive their energy from the quantity and arrangement of live and dead vegetation (fuel) that burns. Fire intensity is further influenced by fuel dryness, weather conditions and topography. Of the factors that determine potential fire intensity, fuel quantity and weather conditions are the most influential, but fuel quantity is the only factor that can be effectively managed. Fuel reduction burning, the practise of purposefully setting low intensity fires under defined conditions of fuel, weather and topography, is a fire management technique to minimise the impact of wildfires by reducing the potential size and intensity of a wildfire, thereby reducing its damage potential and enhancing suppression opportunities. Prescribed burning does not prevent wildfires from occurring but where a significant proportion of the landscape is managed this way, wildfire impact can be considerably reduced. While there are few published cases where this practice has effectively reduced the impact of wildfires and contributed to suppression success (*e.g.* Rodger 1961, Underwood *et al.* 1985, Grant and Wouters 1993), there are numerous unpublished accounts by firefighters and land managers where prescribed burning has ameliorated wildfires (Cheney 1994). However, the practice of prescribed burning for fuel reduction is controversial with concerns that it is ecologically damaging in the long term.

There have been many studies and observations of the ecological effects of a single fire on various plant species and communities in south-west ecosystems, however there are few published data on the long term ecological effects of repeated fuel reduction burning in south-west Australian forests (Christensen and Abbott 1989, Burrows and Wardell-Johnson 2003). Burrows and Wardell-Johnson (2003) reported that 30 years of very frequent burning (3–4 year intervals) of an experimental site in a southern jarrah (*Eucalyptus marginata*) forest did not result in any species losses, but caused changes in the relative abundance of species over time including a decline in the abundance of two obligate seeder species and an increase in abundance of several other species. They also reported that none of the experimental fire regimes favoured all species, including long periods of fire exclusion. There was evidence that burning at 5–7 year intervals in spring and autumn caused no significant changes to species richness or abundance at the study site.

In areas zoned for fuel reduction by prescribed burning, managers aim to maintain fine surface fuel quantity (dead leaves, twigs, bark and floral parts <6 mm in diameter) below about 8 t ha^{-1} and 19 t ha^{-1} for jarrah and karri (*E. diversicolor*) forests respectively. The higher fuel loading for karri reflects its more mesic, hence less flammable condition for a longer period throughout the year (McCaw and Hanstrum 2003). The time taken for fuels to reach these levels, hence the interval between prescribed fires, depends on the rate of fuel accumulation. This varies across the forest region from about 6 to 10 years, depending on site productivity and rainfall (Sneeuwjagt and Peet 1985, Burrows 1994). For example, in most jarrah forests, fine surface fuel quantity reaches *quasi*-equilibrium in 15–17 years (Burrows 1994).

While about 70% of jarrah forest plant species have the capacity to resprout following fire, the remainder depend on seed (obligate seeders), stored either in the soil (soil-stored seeders) or in woody capsules in the canopy (canopy-stored seeders), for regeneration (Christensen and Kimber 1975, Burrows and Wardell-Johnson 2003). An adequate viable seed store and conditions favourable for seed germination and plant growth are essential for flowering plants to persist in an ecosystem that is regularly burnt. For some species, fruit production and seed set may not occur in the first flowering year (Benson 1985, Wark *et al.* 1987, Burrows and Wardell-Johnson 2003) and seed production sufficient to provide adequate seed reserves to restore the population to pref-fire abundance levels may take many years (Gill and McMahon 1986, Gill and Nicholls 1989, Wooller *et al.* 2002). As observed by Gill and Nicholls (1989), seed production is the most relevant measure but flowering is a more practical measure. Gill and Nicholls (1989) suggest that doubling of the juvenile period of a species is a useful guide to when the species is likely to be able to replenish its seed bank following fire. This 'rule of thumb' is consistent with a number of individual species studies of seed production with time (see review by Burrows and Wardell-Johnson 2003). However, there is a paucity of information about the reproductive biology and seed bank dynamics of plant species in Australian ecosystems (Whelan 1995, Burrows and Wardell-Johnson 2003). Until more is known, knowing the juvenile period of species in an ecosystem subjected to regular fire is a useful criterion for determining the minimum fire interval between lethal fires and for assisting with defining ecologically sustainable fire regimes (Tolhurst 1999, Tolhurst 2004). If the interval between fires that are lethal to the parent plants is shorter than the time to first flowering (juvenile period) and seed set, then it is reasonable to assume that obligate seeder species especially, could be at risk of decline. However, if the intensity or patchiness of fires at short intervals is such that parent plants are not killed by fire, then populations may be able to persist and thrive under a regime of frequent but very low intensity, patchy fires.

This paper reports on post-fire regeneration strategies, post-fire juvenile period and flowering phenology of 639 species that occur predominantly in the southern forests and associated ecosystems of south-west Western Australia. We also discuss how other factors such as climate (rainfall), regeneration strategy and life form influence age to first flowering.

Methods

Study sites

Information about post-fire regeneration strategies, flowering time (month) and juvenile period (months) was gathered from study sites in the southern forest region of the south-west of Western Australia (Fig. 1). A brief description of each site is given in Table 1. The McCorkhill and Yendicup forest sites each comprised 10 small (each 4 ha) adjacent plots that were experimentally burnt at various times as part of a broader investigation into the long term effects of fire (see Burrows and Wardell-Johnson 2003). The Lindsay forest site (Table 1) was similar except the plots were smaller (each about 0.5 ha). Data from the Walpole study site (Table 1) were accumulated from some 400 vegetation sample sites located throughout a broad range of vegetation types represented in the Walpole-Nornalup National Park (see Wardell-Johnson *et al.* 1989). Post-fire regeneration strategy and juvenile period were assessed at each site by regular (3–4 weekly) inspections until all species at the site had reached flowering age. The juvenile period is quite variable amongst individuals of the same species in the same population, so we define juvenile period as the time taken for at least 50% of individuals in a population to reach flowering age after fire. This was assessed visually. Visual inspection also ascertained the post-fire regeneration strategy, and plants were classified as shown in Table 2, which has been adapted from Gill (1981). Some species regenerated by more than one of the

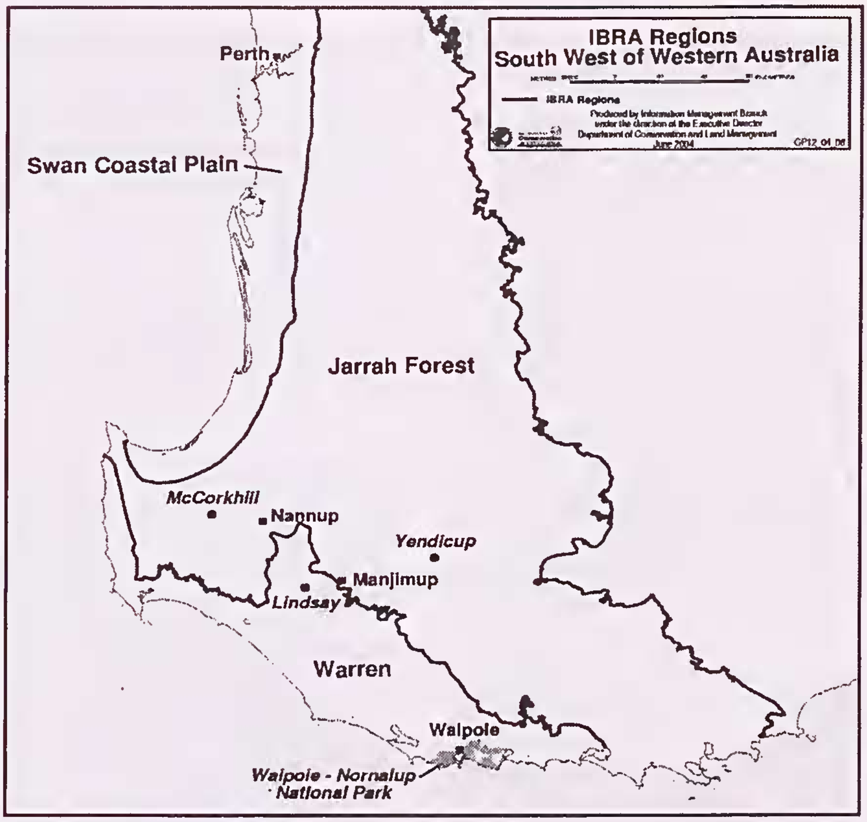

Figure 1. Location of survey sites at McCorkhill forest, Lindsay forest, Yendicup forest and the Walpole-Nornalup National Park in south-west Western Australia from which information about the post-fire juvenile period, regeneration strategy and time of flowering of 639 plant species was gathered.

Table 1

Location and general description of vegetation, soils, landform and climate of sites in south-west Australia forest and associated ecosystems surveyed for post-fire regeneration and flowering responses.

Location	General description of vegetation	Soils and landform	Climate
McCorkhill forest: 20 km west of the town of Nannup. Latitude 33° 57.4' S, Longitude 115° 32.5' E	Havel and Mattiske (2000) vegetation complex type 'Kingia'. Open forest, overstorey dominated by *Eucalyptus marginata* and *Corymbia calophylla* 20–25 m tall. Second storey of *Allocasuarina fraseriana*, *Banksia grandis* and *Persoonia longifolia* to 6 m tall. Low woody shrub and herb understorey to 1 m tall.	Yellow brown gravelly sands on ridges and undulating slopes.	Mediterranean-type climate with cool wet winters and warm dry summers. Mean annual rainfall 1 000 mm.
Lindsay forest: 12 km west of the town of Manjimup. Latitude 34° 14.6' S, longitude 115° 58.0' E.	Havel and Mattiske (2000) vegetation complex type 'Crowea'. Tall open forest of *C. calophylla* and *E. marginata* with some *E. diversicolor* 30–35 m tall. Second storey of *Xylomelum occidentale*, *B. grandis* and *P. longifolia* to 6m tall. Woody shrub and herb understorey to 1.5 m tall.	Yellow duplex soils with pale brown sandy loam topsoil on ridges and midslopes.	Mediterranean-type with cool wet winters and warm dry summers. Mean annual rainfall 1 150 mm.
Yendicup forest: 45 km west of the town of Manjimup. Latitude 34° 11.6' S, longitude 116° 37.0' E.	Havel and Mattiske (2000) vegetation complex type 'Frankland Hills'. Woodland of *E. marginata* and *C. calophylla* 15–20 m tall. No significant second storey. Open woody shrub and herb understorey to 0.5 m tall.	Yellow brown gravely duplex soils with some laterite boulders.	Mediterranean-type with cool wet winters and warm dry summers. Mean annual rainfall 750 mm.
Walpole-Nornalup National Park: 18 390 ha on the south coast of Western Australia. Surrounds the town of Walpole	Wardell-Johnson *et al.* (1989) described 15 vegetation communities including a variety of heathlands, woodlands, low open eucalypt forests and tall eucalypt forests.	Diversity of soils and landforms. See Wardell-Johnson *et al.* (1989) and CALM (1990).	Mediterranean type climate with cool wet winters and mild summers. Mean annual rainfall varies across the Park from 1 200–1 300 mm.

Table 2

Classification of post-fire regeneration strategies of vascular plants in south-west Australia ecosystems (adapted from Gill 1981).

Seeders	Resprouters
(1) Stem girdling or 100% scorch kills, depends on canopy stored seed	(4) Survives stem girdling or 100% scorch, soil suckers (rhizome, corm, bulb, tuber)
(2) Stem girdling or 100 % scorch kills, depends on soil stored seed	(5) Survives stem girdling or 100% scorch, basal sprouts (lignotuber)
(3) Stem girdling or 100% scorch kills, no stored seed	(6) Survives 100% scorch, epicormic shoots
(8) Stem girdling or 100% scorch kills, any of 1,2,3 above	(7) Survives 100% scorch, large apical bud
(10) Ferns and Allies (spores)	(9) Survives 100% scorch, any of 4,5,6,7 above

categories shown above. For example some lower tree and overstorey tree species in particular, including *Banksia grandis* and *Eucalyptus marginata*, were capable of resprouting from either a subterranean lignotuber or epicormic buds, or of regenerating from seed, depending on the fire intensity and the physiological age of the plant (Burrows 1985). In these cases, species were deemed to be resprouters and allocated to one of the resprouter categories shown in Table 2. Some thin barked tall shrub species that are typically characterised as obligate seeders, such as *Melaleuca viminea*, have occasionally been observed to resprout following very low intensity fire which scorched the canopy but did not girdle the main stem. Such species were classified as obligate seeders in this study.

Results

Information on post-fire regeneration strategy, juvenile period and peak flowering month was documented for 639 plant species representing 249 genera and 72 families (Table 3). The most commonly observed families were Orchidaceae, Proteaceae, Papilionaceae, Myrtaceae, Epacridaceae, Asteraceae and Mimosaceae. The least commonly observed families included Portulaceae, Cephalotaceae, Lindsaeaceae, Zamiaceae, Loranthaceae, Podocarpaceae and Dennstaedtiaceae. At the intermediate and high rainfall sites (McCorkhill forest near Nannup, Lindsay forest near Manjimup and Walpole-Nornalup National Park), all upland forest understorey species reached flowering age within in 3 years of fire, with most (90%) flowering within 2 years (Fig. 2). At the lower rainfall site (Yendicup forest near Perup) all upland forest understorey species reached flowering age within 4 years of fire. Of the 639 species observed, 17 (3%) species had juvenile periods >3 years and three species were observed to take longer than 4 years to reach flowering after fire. These were *Banksia brownii* (5 yrs), *B. seminuda* (5 yrs) and *Melaleuca viminea* (5 yrs) (Table 4). Species with longer juvenile periods were mostly

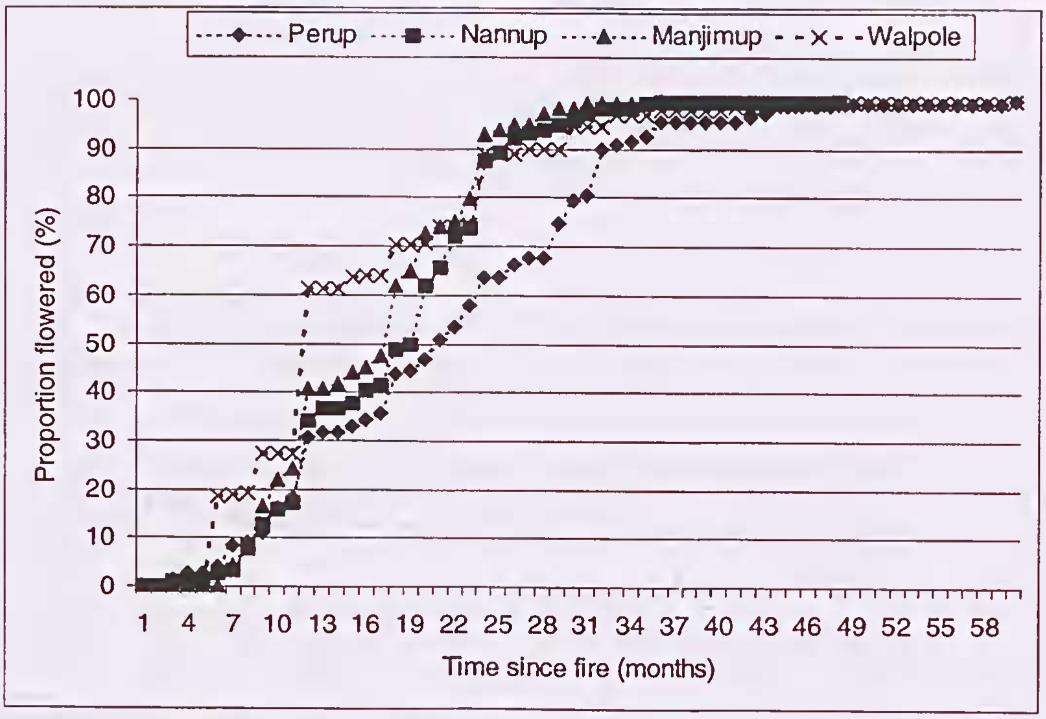

Figure 2. Cumulative proportion of species to have reached flowering age with time since fire for 639 species from four locations in the south-west forest region of Western Australia. A species was deemed to have reached flowering age when at least 50% of the population had flowered.

Table 3

Plant families surveyed ranked by number of species in each family

Family	No. Genera	No. Species
Orchidaceae	20	76
Proteaceae	19	64
Papilionaceae	18	59
Myrtaceae	17	46
Epacridaceae	9	28
Asteraceae	18	28
Mimosaceae	2	27
Poaceae	15	23
Stylidiaceae	2	23
Goodeniaceae	6	20
Cyperaceae	9	16
Apiaceae	9	16
Dilleniaceae	1	16
Dasypogonaceae	5	15
Anthericaceae	8	15
Rutaceae	5	13
Thymelaeceae	1	9
Haemodoraceae	3	9
Droseraceae	1	8
Restionaceae	6	8
Sterculiaceae	3	6
Lobeliaceae	1	6
Tremandraceae	3	6
Iridaceae	2	6
Colchicaceae	2	6
Polygalaceae	2	5
Lamiaceae	2	5
Santalaceae	3	4
Haemodoraceae	1	4
Euphorbiaceae	4	4
Loganiaceae	2	4
Rubiaceae	1	3
Pittosporaceae	2	3
Rhamnaceae	2	3
Casuarinaceae	1	3
Lentibulariaceae	1	3
Haloragaceae	2	2
Stackhousiaceae	2	2
Xanthorroeaceae	2	2
Lauraceae	1	2
Ranunculaceae	2	2
Phormiaceae	2	2
Geraniaceae	2	2
Scraphylariaceae	2	2
Solanaceae	1	2
Campanulaceae	1	2
Hypoxidaceae	1	2
Onagaceae	1	2
Amarathaceae	1	2
Caesalpiniaceae	1	1
Gyrostemonaceae	1	1
Violaceae	1	1
Phormiaceae	1	1
Centrolepidaceae	1	1
Aspleniaceae	1	1
Linaceae	1	1
Malvaceae	1	1
Brassicaceae	1	1
Primulaceae	1	1
Olacaceae	1	1
Saxifragaceae	1	1
Byblidaceae	1	1
Maryanthaceae	1	1
Sapindaceae	1	1
Xyridaceae	1	1
Portulaceae	1	1
Cephalotaceae	1	1
Lindsaeaceae	1	1
Zamiaceae	1	1
Loranthaceae	1	1
Podocarpaceae	1	1
Dennstaedtiaceae	1	1
Total: 72	249	639

canopy-stored seeders that occurred in less flammable habitats such as moist parts of the landscape (*e.g.*, riparian zones, some swamps) or where surface fuels were discontinuous or sparse (*e.g.*, rock outcrops, some swamps) (Table 4).

Intra-species variation in juvenile period was evident locally and regionally with plants growing in the lower rainfall areas often taking considerably longer to flower than the same species at higher rainfall sites. Some examples are shown in Table 5.

Mean juvenile period, or secondary juvenile period in the case of resprouters (Gill 1975), for various plant life forms is shown in Table 6. As to be expected, trees, lower trees and woody shrubs took longer to flower after fire than geophytes, grasses and annual herbs. All overstorey tree species (*Eucalyptus* spp.) and many lower tree species (*e.g.* some *Banksia* spp.) were capable of both re-sprouting and regenerating from seed after fire; the juvenile period reported here is for mature plants that have re-sprouted. The juvenile period of plants regenerating from seed would be considerably longer (probably 10–20 years for eucalypts). There was a statistically significant difference (á = 0.05) in juvenile period between seeders and resprouters in almost all life form categories with resprouters flowering sooner than obligate seeders, the exception being grasses, where seeders flowered sooner. Mean juvenile period for plants in each of the nine post-fire regeneration categories is shown in Figure 3. Overall, canopy-stored seeders had the longest juvenile period (mean about 36 months) and geophytes (especially Orchidaceae, Droseraceae) and plants with large apical buds (Xanthorroeaceae and Dasypogonaceae) took the shortest time to flower (mean about 10 months). *Kingia australis* (Dasypogonaceae) had the shortest juvenile period with most of the population flowering within 2 months of fire; plants with stems shorter than about 100 cm had few or no flowers, suggesting they had not reached reproductive maturity.

While flowering occurred throughout the year, there is a distinctive flowering peak during spring when about 60% of plants flower. Few plants flowered during the

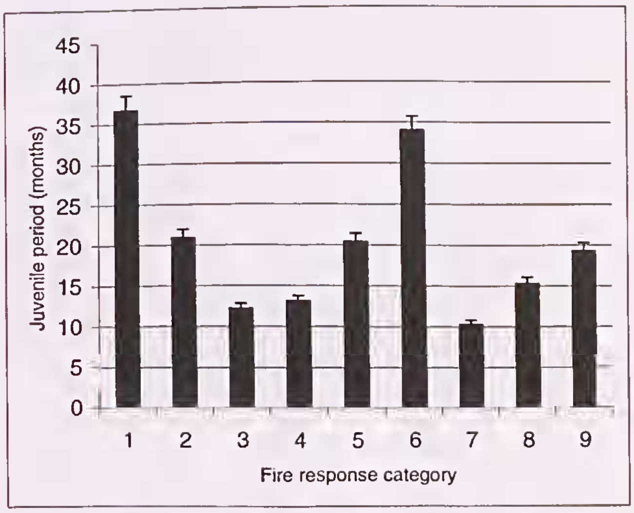

Figure 3. The mean juvenile period for plant species categorised according to post-fire regeneration response strategy. Fire response categories are shown in Table 2.

Table 4

Shrubs and small trees species with known juvenile periods > 3 years. Habitat flammability rating takes account of seasonal moisture regime and fuel characteristics including quantity, structure and continuity.

Species	Conservation Status	Post-fire regeneration strategy	Juvenile period (months)	Distribution and Habitat	Habitat Flammability Rating
Acacia pentadenia Lindl.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	36 (Pemberton) 48 (Walpole-Nornalup NP)	Southern jarrah and karri forests and coastal areas. Loamy soils, moist and swampy areas.	LOW: High fuel accumulation rate but fuel complex stays moist for long periods of the year. Note: Juvenile period variable across range, depending on site productivity.
Banksia brownii R.Br.	Declared rare	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Walpole-Nornalup NP)	Restricted distribution, Walpole-Nornalup NP-Albany. Rock outcrops, gullies.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry windy conditions for fire spread.
Banksia meisneri Lehm.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (McCorkhill forest)	Throughout the lower south-west, Busselton to Katanning. Swamp margins, seasonally wet flats.	MODERATE: Fuel complex stays moist for longer period, low sparse surface fuels, often dense elevated heath fuels requiring wind for spread.
Banksia occidentalis R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (McCorkhill forest) 36 (Walpole-Nornalup NP)	South coast and adjacent hinterland, Augusta to Esperance. Low lying areas, swamps, seepages, consolidated sand dunes.	MODERATE: Fuel complex stays moist for longer period, low sparse surface fuels, often dense elevated heath fuels requiring wind for spread. Note: Juvenile period variable across range, depending on site productivity.
Banksia quercifolia R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Walpole-Nornalup NP)	South coast and adjacent hinterland, Pemberton to Albany. Swamps, seasonally wet flats.	MODERATE: Fuel complex stays moist for longer period, low sparse surface fuels, often dense elevated heath fuels requiring wind for spread.
Banksia seminuda (A.S. George) Rye	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Walpole-Nornalup NP)	Throughout lower south-west, Dwellingup to Albany. Riverine, consolidated dunes, rock outcrops.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.
Banksia verticillata. R.Br.	Declared rare	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Walpole-Nornalup NP)	South coast, Walpole- Nornalup NP to Albany. Rock outcrops.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
Calothamnus rupestris Schauer	Priority four	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Northern jarrah forest)	Rock outcrops in the northern jarrah forest.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
Dryandra lindleyana Meisn.	Not threatened	Survives stem girdling or 100% scorch, soil suckers (rhizome, corm, bulb, tuber)	42 (Yendicup forest) 32 (McCorkhill forest)	Widespread throughout south-west, Geraldton to Albany. Habitat variable across range.	HIGH: Commonly occurs in midslope and upland jarrah forests and woodlands with continuous cover of surface fuel. Note: Juvenile period variable across range, depending on site productivity.

Grevillea occidentalis R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	44 (Yendicup forest)	Lower south-west and south coast, Walpole- Nornalup NP to Albany. Sand over laterite or granite, loam, gravel.	LOW-MODERATE: Commonly occurs in jarrah woodlands and swamp margins. Low fuel accumulation rates.
Hovea trisperma Benth.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	42 (Yendicup forest) 22 (McCorkhill forest)	Widely distributed throughout south-west forests and south coast. Variety of habitats across range.	Occurs in a wide range of fuel complexes. Note: juvenile period variable across range, depending on site productivity.
Lambertia orbifolia C.A.Gardner	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	40 (Scott River)	Restricted distribution, coastal areas- Busselton, Margaret River, Albany. Creeksides, dunes, swamps.	LOW: Coastal heaths, swamps, wet areas. Requires dry, windy conditions for fire spread.
Lambertia rariflora Meisn. subsp. *lutea* Hnatiuk	Priority three	Stem girdling or 100% scorch kills, depends on soil-stored seed	48 (Walpole-Nornalup NP)	Restricted distribution Walpole-Nornalup NP region. Creeksides, seasonally wet areas, occasionally mid-slopes and ridges.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.
Lambertia rariflora Meisn. subsp. *rariflora*	Priority four	Stem girdling or 100% scorch kills, depends on soil-stored seed	48 (Margaret River)	Restricted distribution Busselton-Margaret River area. Creeksides.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.
Lasiopetalum floribunda Benth.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	44 (Yendicup forest) (24 Lindsay forest)	Widespread throughout forest region	Occurs in a wide range of fuel complexes. Note: juvenile period variable across range, depending on site productivity.
Leucopogon pulchellus Sond.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	43 (Yendicup forest) 30 (McCorkhill forest)	Northern and central jarrah forests. Mainly lateritic or granitic soils.	HIGH: Occurs in tall forest and woodland fuel complexes. Note: juvenile period variable across range, depending on site productivity.
Melaleuca thymoides Labill.	Not threatened	Survives stem girdling and 100% scorch, basal sprouts (lignotuber)	44 (Yendicup forest) 20 (McCorkhill forest)	Widespread throughout south-west forests and great southern, Perth to Esperance. Winter wet depressions, granite hills, sand dunes.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions. Note: juvenile period variable across range, depending on site productivity.
Melaleuca viminea Lindl.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Yendicup forest)	Widespread throughout the south-west from Geraldton to Esperance. Creeksides, winter wet depressions, rocky coastal areas, flats.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
Taxandria juniperina (Schauer)J.R.Wheeler & N.G.Marchant	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Pemberton)	South coast and adjacent hinterland from Busselton to Albany. Watercourses and swamps.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.

Table 5

Examples of intra-species variation in juvenile period (months) with variation in mean annual rainfall

Species	Low rainfall (750 mm annum^{-1})	High and intermediate rainfall (1 000–1 350 mm annum^{-1})
Agrostocrinum scabrum (R.Br.) Baillon	20	12
Allocasuarina humilis (Otto & F.Dietr.) L.A.S.Johnson	35	24
Astroloma drummondii Sonder	24	12
Billardiera variifolia DC.	26	12
Bossiaea linophylla R.Br.	36	24
Clematis pubescens Endl.	32	18
Conospermum caeruleum R.Br.	32	12
Daviesia preissii Meisn.	30	12
Gompholobium tomentosum Labill	31	20
Hakea amplexicaulis R.Br	30	18
Hibbertia rhadinopoda F.Muell.	21	12
Lasiopetalum floribunda Benth	44	24
Melaleuca thymoides Labill.	44	24
Petrophile diversifolia R.Br.	36	26
Velleia trinervis Labill.	32	20

Table 6

Mean time (months) to first flowering after fire (juvenile period) for various life form categories and by primary post-fire regeneration strategy. Standard errors in parentheses.

Life form	Regeneration strategy	
	Seeders	Resprouters
Tree or lower tree	49.5 (2.7)	36.9 (2.0)
Woody shrub	24.8 (0.7)	20.7 (0.5)
Perennial herb	15.0 (1.0)	14.5 (0.7)
Short-lived herb	11.3 (0.8)	None observed
Grass	9.7 (1.2)	13.9 (1.2)
Sedge	None observed	15.8 (1.2)
Geophyte	None observed	10.3 (0.3)

late autumn and winter months (Fig. 4). The number of plant species in each of the post-fire regeneration categories and for three broad rainfall zones is shown in Table 7. Overall, about 70% of plants resprouted following fire and about 30% regenerated from seed. Only 1–2% of species relied on seed stored in the canopy (canopy-stored seeders) whereas 25–30% relied on seed stored in the soil (soil-stored seeders).

Discussion

An ability to flower and to produce viable seeds in inter-fire periods is fundamental to the persistence of vascular plants in fire-prone environments, especially those that depend on seed stored on the plant (canopy-

Table 7

The number and proportion (%) of species in each post-fire response category for three rainfall zones of the south-west forests and associated ecosystems.

Post-fire regeneration strategy	McCorkhill forest Low rainfall (~750 mm annum^{-1})	Yendicup forest Intermediate rainfall (~1 000 mm annum^{-1})	Lindsay forest and Walpole-Nornalup National Park High rainfall (~1 150–1350 mm annum^{-1})
1. Stem girdling or 100% scorch kills; canopy stored seed	3 (1.7%)	4 (1.5%)	5 (1.3%)
2. Stem girdling or 100% scorch kills; soil stored seed	46 (26.6%)	69 (25.6)	114 (30.2%)
3. Stem girdling or 100% scorch kills; no stored seed	0 (0%)	1 (0.3%)	3 (0.8%)
4. Survives stem girdling or 100% scorch; soil suckers (rhizome, corm, bulb, tuber)	52 (30.2%)	69 (25.6%)	133 (35.3%)
5. Survives stem girdling or 100% scorch; basal sprouts (lignotuber)	60 (34.7%)	99 (36.6%)	79 (20.2%)
6. Survives 100% scorch; epicormic shoots	3 (1.7%)	15 (5.5%)	14 (3.7%)
7. Survives 100% scorch; large apical bud	2 (1.2%)	5 (1.8%)	3 (0.8%)
8. Stem girdling or 100% scorch kills; any of 1,2,3 above	6 (3.4%)	5 (1.8%)	21 (5.6%)
9. Survives 100% scorch, any of 4,5,6,7	1 (0.5%)	2 (0.6%)	3 (0.8%)
10. Ferns and Allies (spores)	0 (0%)	1 (0.3%)	2 (0.5%)
Total	173 (100%)	270 (100%)	377 (100%)

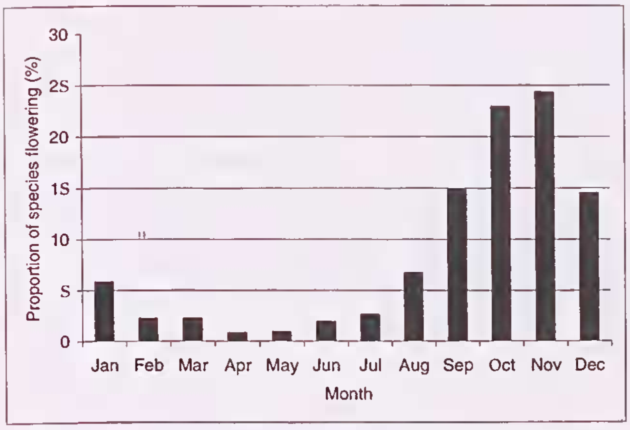

Figure 4. Proportion of species flowering in each month of the year.

stored seeders). While these species make up only 1–2% of all species observed (Table 6), they are often threatened taxa, have a limited distribution or are thicket forming, keystone species providing important habitat for other organisms. Of the 639 species observed in this study, 619 (~97%) reached flowering age within three years of fire, and all species had flowered within 5 years of fire. While this sample (639) is about a quarter of the known flora of the region, it represents a cross-section of habitat types, life forms and of taxa. This relatively rapid post-fire growth and maturation (short juvenile period) is not surprising given these ecosystems have a very long association with fire. Understorey species with juvenile periods longer than 3 years were confined to either the less productive lower rainfall zones of the forest region or to less flammable habitat elements in the landscape. The importance of climate (especially rainfall) in influencing juvenile period is further evidenced by the intra-specific variation shown in Table 5. Habitat flammability is broadly determined by the seasonal rhythm of moisture regime (McCaw and Hanstrum 2003) or by the quantity, structure and continuity of the vegetation complex, which becomes fuel for a bushfire. Parts of the landscape that stay moist for longer periods, such as some riparian zones, valley floors and swamp complexes, have a shorter period of the year when live and dead vegetation (fuel) is sufficiently dry to sustain fire, therefore a lower probability of combusting, so it is not surprising that species with longer juvenile periods most often occur in these areas. Other flat or low-lying, moisture gaining parts of the landscape, such as some myrtaceous swamps, are highly flammable for long periods of the year because of greater exposure to wind and solar radiation and because of the nature, structure and quantity of the elevated vegetation. However, it is unusual to find species with long juvenile periods in these habitats. Habitats with low or discontinuous fuels (such as rock outcrops and some swamp and woodland complexes) usually only carry fire under dry and windy conditions, further limiting the time throughout the year when conditions are such that these areas can burn. Thus, and as to be expected, understorey species with longer juvenile periods (>3 years) occur in habitats that are less prone to fire and are commonly tall shrubs and lower tree species such as Banksia spp. (Table 4). On the other hand, plants with long juvenile periods are rarely found in parts of the landscape that are more prone to fire because these habitats are drier for longer periods and support continuous surface fuels, such as forested plateaus and uplands (see Table 4). Clarke (2002) working in south-east Australian forest ecosystems reported that rock outcrops and pavements were dissimilar in species composition from the surrounding forest and were dominated by shrubs that were readily killed by fire and depended on post-fire seedling recruitment. In contrast, the most abundant species in the adjacent, more flammable forest, were post-fire resprouters.

Muir (1987) found that of the 198 plant species he observed throughout the south-west, mid-west, wheatbelt, south coast and goldfields regions of Western Australia, almost 74% flowered within 4 years of fire, but about 26% took 5–8 years to flower. Of the species that took 5–8 years to flower, 7 (13%) occurred in the forest region, the remainder occurring in the lower rainfall areas outside the forest region. Of these, four are resprouters (*Agonis flexuosa, Astartea fascicularis, Banksia grandis* and *Regelia ciliata*), which we recorded flowering 24–36 months after fire, and the remainder (*Casuarina obesa, Melaleuca diosmifolia* and *M. laterita*) occur in or around swamps or winter-wet depressions. Van der Moezel *et al.* (1987) documented the juvenile period of 192 species of the northern sandplain kwongan near Badgingarra (mean annual rainfall about 500 mm) and reported that 79% of species flowered within 2 years of fire, with all species observed flowering within 5 years of fire. These data support the proposition that mean annual rainfall and spatial and temporal variability in landscape flammability are significant factors influencing the distribution of fire regime sensitive plant species, which are mostly obligate seeder species with relatively long juvenile periods.

Fine surface fuel (dead leaves, twigs, bark, fruits) on the forest floor provides the dominant fuel layer because of its position (at the base of the fuel ladder), quantity and continuity (Burrows 1994). Forest fires are unlikely to spread when the surface fuel moisture content exceeds about 21% or when the surface fuel quantity is below about 4 t ha^{-1} (Burrows 1994). Under extreme fire weather conditions, which are likely to occur on only 1–2 days each year (McCaw and Hanstrum 2003), fire spread may be sustained when the surface fuel quantity is as low as 3 t ha^{-1} but fires are generally low intensity and patchy. Surface fuels in upland jarrah forests re-accumulate to 4 t ha^{-1} in about 2.5 – 4 years, depending on the structure and productivity of the forest (Fig. 5). From Figure 5, it can be seen that the shortest time after fire that jarrah forests will re-burn (2.5 – 4 yrs) is similar to the juvenile period of the slowest maturing understorey plants (3 – 4 years) shown in Figure 2. This is unlikely to be coincidence; it is likely that plants with longer juvenile periods, particularly obligate seeders, have been unable to persist in habitats that have the potential to re-burn at 3–4 year intervals. In the forest region, plants with longer juvenile periods are confined to habitats that have a lower probability of burning because of favourable moisture regimes or because of the discontinuous structure of the fuel complex, as discussed above.

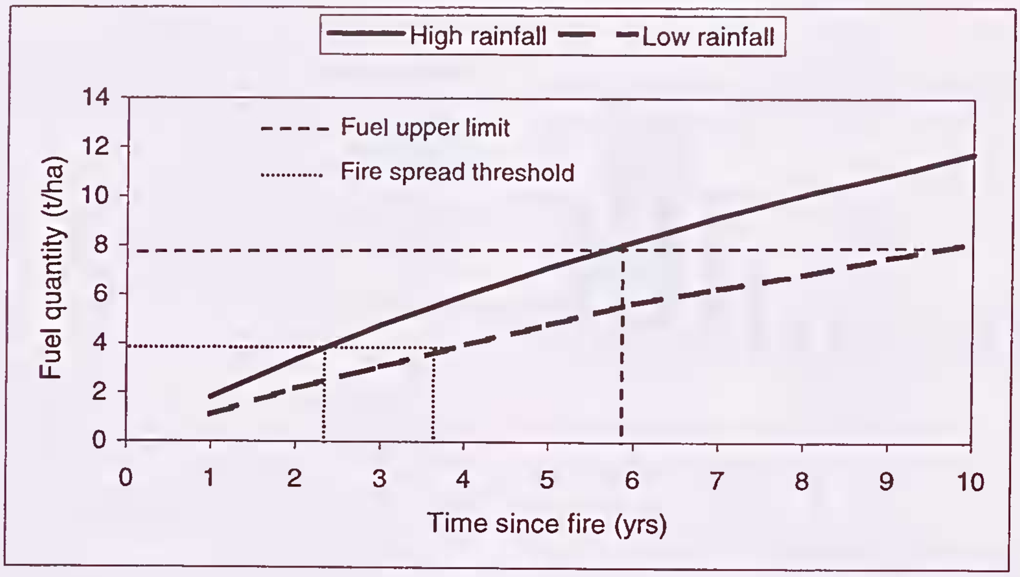

Figure 5. Fine surface fuel accumulation rates for high rainfall (Lindsay forest) and low rainfall (Yendicup forest) jarrah forests. The fuel upper limit is the quantity below which fuels are maintained by prescribed burning in strategic areas to assist wildfire control. The fire spread threshold is the fuel quantity below which fire spread is unlikely.

Management implications

Prescribed burning for fuel management in jarrah forests aims to maintain fine surface fuel quantities in strategic areas below about 8 t ha^{-1} (McCaw and Burrows 1989). Knowledge of fire behaviour and operational experience has shown that fires burning in heavier fuels and under warm, dry and windy conditions in summer are difficult, dangerous or impossible to control (Underwood *et al.* 1985), cause considerable physical damage to forest ecosystems (Peet and Williamson 1968 and Burrows 1987) and generally burn most of the landscape, leaving few if any, unburnt patches. The time taken for fine surface fuels to re-accumulate to 8 t ha^{-1} varies depending on the structure and productivity of the forest, which is largely dependent on annual rainfall as shown in Figure 5. For example, at the Lindsay forest site (high rainfall jarrah forest) fine surface fuels reach about 8 t ha^{-1} some 6 years after fire, whereas it takes about 10 years at the Yendicup forest site (low rainfall jarrah forest). This is 2–2.5 times the juvenile period of the slowest maturing understorey plants and 3–3.5 times the juvenile period of 90% of plants in these ecosystems. While there is a paucity of information on seed bank dynamics and seed longevity in fire prone ecosystems, some species are able to produce considerable quantities of viable seed in the first or second flowering years. These include species with short life cycles, such as annual grasses and herbs, species that rely on the production of non-dormant seed to take advantage of post-fire establishment conditions, so mainly flower in the first few seasons after fire (Johnson *et al.* 1994, Denham and Auld 2004) and so-called native 'fireweeds', perennial herbs and shrubs (often leguminous) that regenerate profusely after fire, grow and mature rapidly and are usually relatively short-lived (Bell *et al.* 1989). However other plants, notably serotinous and partially serotinous *Banksia* species, produce low levels of viable seed in the first few years after flowering (Kelly and Coates 1995, Enright *et al.* 1996, Wooller *et al.* 2002). Gill and Nichols (1989) and Burrows and Wardell-Johnson (2003) have recommended that, for plant conservation, the conservative minimum interval between lethal fires for a particular ecosystem should be twice the juvenile period of the slowest maturing fire sensitive plant species in the ecosystem, where juvenile period is the time taken for at least 50% of the population to reach flowering age. This 'rule of thumb' is consistent with the limited number of seed bank dynamics studies that have been conducted in fire-prone environments including south-west Western Australia (see review by Burrows and Wardell-Johnson 2003). Therefore, in forested uplands and other flammable habitats within the landscape, the conservative minimum fire interval between lethal fires is about 6–8 years, depending on the productivity of the site (Fig. 2). However, in less flammable parts of the landscape (rock outcrops, riparian systems, some wetlands), where plants with longer juvenile periods are most likely to occur, the conservative minimum interval between lethal fires is probably 10–12 years.

Fire sensitive plants with long juvenile periods can survive shorter fire intervals if fires are of a very low intensity (non-lethal to the plant) and patchy (do not burn the plant population). Such fires are only possible when burning conditions are near the threshold for fire spread, that is, when fuel quantities are low (Fig. 5), or when fuels are moist. Low fuel quantities can only be maintained by the frequent introduction of fire into the landscape. Frequent patch-burning of the landscape should eventually result in a fine scale mosaic of patches of vegetation at different post-fire stages, ranging from recently burnt to long unburnt. This proposition requires further investigation in the field. South-west landscapes are a mosaic of a variety of landforms and associated vegetation assemblages, including habitats that contain plants with long juvenile periods requiring longer intervals between fires. As these habitats are less flammable, either because they remain wetter for longer, or contain less flammable fuel complexes, prescribed burning can be planned and implemented under seasonal and diurnal weather conditions to exploit these temporal and spatial flammability differentials, thereby reducing the risk of burning fire sensitive species and communities too frequently. In south-west forest landscapes, low intensity prescribed fires set under moist conditions in spring usually burn the drier parts of the landscape, such as forested uplands, but often do not burn riparian zones and areas of sparse fine surface fuels such as rock outcrops. The proportion of the landscape that is sufficiently dry to burn increases rapidly with the onset of summer drying and where fuels are continuous, fires in summer and autumn usually burn the entire landscape.

Conclusion

Juvenile period can be used as a biological indicator to help determine ecologically acceptable minimum intervals between fires in various ecosystems. The post-fire juvenile period of understorey plants in south-west forests and associated ecosystems reflects site productivity, as expressed by rainfall, and habitat flammability, as determined by seasonal moisture regime and fuel characteristics. Plants with longer juvenile periods are most likely to occur in the lower rainfall regions, and in less flammable habitats such as riparian zones, rock outcrops and some wetlands. At the landscape scale, the minimum ecologically acceptable fire interval will vary across the landscape in response to changing habitat types. In the interests of plant conservation, fire management, particularly the interval between prescribed fires, should aim to accommodate this variability.

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